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Mangrove Macroalgae: A Review of Australian Studies

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Algae associated with mangroves have received particular attention in phycology since Dr. Erika Post recognised the distinctive nature of the macroalgal community and began a series of papers (1936-1968) on their systematics and distribution. This address reviews Post's studies on the taxonomy and systematics of the algae of the *Bostrychia-Caloglossa* association especially as they relate to Australia, and then reviews the contribution of Australian studies on the taxonomy, ecology, ecophysiology, distribution and biogeography of mangrove macroalgae.

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INTRODUCTION

The recognition of mangrove macroalgae as a distinct field of study within phycology dates from Post (1936a) and her major paper on the systematics and biogeography of what she termed the *Bostrychia-Caloglossa* association. Her use of the term association was general, in the sense of an assemblage, rather than in the rigorous sense it is now used in ecology. Since that time there has been a wide recognition of the distinctive nature of these algal communities with numerous papers by Post and others on floristics. Partly this reflects general trends in algal ecological studies since the 1970s which have placed increasing emphasis on algae of estuaries and soft bottom shores rather than those of rocky shores, on production biology, and studies of tropical ecosystems (King 1990a). In this review, a number of different types of studies will be considered: taxonomy and systematics, floristics and biogeography, local distribution, productivity and biomass, and ecophysiology especially in relation to salinity. Given the pivotal role played by Post in her series of papers (Post 1936a *et seq.*) it is appropriate to consider her studies first.

THE CONTRIBUTION OF ERIKA POST

Erika Post's entire scientific career was concerned with the study of the macroalgae associated with mangrove and saltmarsh communities, and she published some 34 papers on the subject over the period 1936-1968. All of her papers were single author publications and with one exception written in German. A full list of her publications is given in the bibliography.

Post's first and major contribution (Post 1936a) presented the results of the algal collections of the 1929 German Scientific Expedition in the Sunda region and was based on collections of Prof. W. Troll. Recognising the need for a reassessment of the taxa involved she undertook a complete revision of three major taxa *Bostrychia*, *Caloglossa* and *Catenella*. Later papers extended this approach but with an emphasis on distributional studies. *Caloglossa* later received further detailed attention (Post 1943) and two new species of *Bostrychia* were also described (Post 1939a, 1941). A major review of work was

published in 1963.

Post lived in Kiel (Schleswig-Holstein, Germany) but had no formal attachment with either the Marine Sciences Institute (Institut für Meereskunde) Kiel or the Botanical Institute of the Christian Albrechts Universität in Kiel. Despite this limitation Post almost single handedly promoted a global view of the study of the taxonomy, morphology and geographic distribution of mangrove algae. It was she who coined the terms '*Bostrychietum*' and '*Bostrychia – Caloglossa* Assoziation'. In retrospect it is easy perhaps to criticise certain aspects of Post's taxonomic works. She appears to have given little attention to typification of species and failed to adhere strictly to the rules of taxonomic nomenclature. In addition she was unable to fully appreciate variation within taxa. However, as King and Puttock (1989) have pointed out for *Bostrychia*, Post was consistent in her use of names throughout her papers and hence it is comparatively easy to correlate her species names with more recent taxonomy.

Post's major contributions were concerned with the systematics and distribution of mangrove algae, although she did report ecological observations albeit based on herbarium labels and correspondence from collectors. Unfortunately many of her later papers are little more than extensive lists of species and localities based on such sources. The fact that data are often presented in the form of a compilation rather than a synthesis and in German means that these valuable data remain relatively under-utilised. Some of the later papers, however, do address particular biological issues such as the ability of typical mangrove algae to withstand desiccation (Post 1963c) and to grow at a range of salinities in the natural environment (Post 1963d).

From the beginning Post was in contact with phycologists and collectors around the world and maintained a prodigious correspondence. In her first paper she thanked 95 individuals for their help in providing literature and material. That list reads like a 'Who's Who' of phycology at the time. Included are Prof. A.H.S. Lucas (Girrahween), Prof. E. Nicholes (Crawley) and Prof. F.J. Rae (Melbourne) from Australia, and Dr. L.M. Cromwell (Auckland) and Dr. R.M. Laing (Christchurch) from New Zealand. Post never visited Australia or New Zealand, nor would it appear ever made any field collections in mangroves. Nonetheless on the basis of her extensive correspondence she wrote a number of papers about algae in specific areas: in the Australasian region, New Zealand (Post, 1936b, 1966b) and Australia (Post 1964c). The last of these papers, somewhat oddly entitled '*Bostrychietum* aus dem National Park von Melbourne', is based on collections made by Sophie C. Ducker at Wilsons Promontory, Victoria (with comparisons made with earlier collections of among others A.B. Cribb, F. von Mueller, H.T. Tisdall and H.B.S. Womersley) and a collection by Dr. J.A. Carnahan from the Minnamurra River (with comparisons made to Valerie May's collections in the Georges River estuary).

Post continued her correspondence throughout the 1960s collecting both literature and specimens. An example of the former is the following request to R.H. Anderson, Royal Botanic Gardens and National Herbarium, Sydney and dated 21st July 1961:

'Dear Mr. Anderson,

I try now already a very long time to get some papers of AHS Lucas of which I only would be interested in the verbally text (& figures?) for all what is said about *Bostrychia* (= *Amphibia*), *Caloglossa* (= *Delesseria lepieurii*) and *Catenella* (& *Murrayella*) and I would be very grateful to you for the corresponding photocopies which of course I will pay.

The papers in questions are:

- 1) Lucas and Perrin F.: The seaweeds of South Australia Part II. Red Seaweeds. Handbook of the flora & fauna of South Australia, Adelaide, p. 111-458, 202 figures (Are they also mentioned in the 'Introduction' in Part I, 1936?)
- 2) Lucas A.H.S.: Marine Algae in 'British Association for the Advancement of Science) Handbook for N.S. Wales', p.459-463.

I have no idea, if there are some more recent publications in which my genera are mentioned.

In the hope of your kind help believe me.

Yours faithfully,
E. Post.'

Her requests for algal material were quite specific and with details such that a non-phycologist might respond appropriately. In a letter (17 May 1965) to Dr. Knowles Mair [Director of the Royal Botanic Gardens, Sydney 1964-1970] to thank him for recent correspondence she noted:

'Of course I would also be interested in N.S.W. (dried material of the small blackish-purple mosslike mangrove algae (a) feathery, b) leafy, c) rosary like) which grow (mostly) in thick clusters on dead stumps, tree bases and the upper portions of the pneumatophores, uncovered between tides, if possible from any locality except Hawkesbury River, Kirribilli Point, Ryde, Abbotsford, Gladesville, Cook's River, Georges river and Minnamurra River estuary. Please leave the tufts just as they are (unsorted).

Believe me,

Yours faithfully,
E. Post.'

Predictably it was Valerie May [Jones] (King and Briggs 1988) who answered both of these requests noting when posting the collected materials (22/9/65) that:

'Many of our mangrove areas are being destroyed, bridges, embankments, parking lots replace former collecting areas and even those collections I have been able to make are often from ecologically damaged areas, suffering from much silting up. Some areas, such as Georges River Bridge, where I collected material for you some years ago, have no signs of mangroves left now, only stone embankments. In other areas such as at Roseville Chase, Sydney, the mangroves still remain after bridge building but they now stand in a firm substrate and there is no trace of their characteristic algal flora, — oyster shells replacing it. Several areas from which I have collected this time are so silty — due to man's activity — that I expect the algal flora to disappear relatively soon'.

Whether or not that algal flora has gone, what has disappeared are the extensive collections which formed the basis of Post's work. As already noted Post had no formal relationship with any scientific institutions. Following her death in 1980 her apartment was cleared and only late in that process were staff of the Marine Sciences Institute, Kiel involved. Her reprints and papers on mangrove algae of the southern hemisphere are now in my collection. Included in her possessions was a small compound microscope of unknown manufacture about which Mr. R. Oldfield (pers comm.) has provided the following information. "This compound drum microscope was probably made in Britain between 1840 and 1890 and could equally as well have been sold in a toy shop as by an optician. Cost: 16s 0d retail/9s 6d wholesale. It had three single screw on lenses which could be combined". Whether or not this instrument was Erika Post's research microscope, her lack of facilities was real, and her major contribution in mangrove algal studies is therefore especially noteworthy.

FLORISTICS

Post (1936a *et seq.*) drew attention to the characteristic algal flora associated with mangroves, the *Bostrychia* – *Caloglossa* – association consisting of *Bostrychia* (now including *Stictosiphonia* — see King and Puttock 1989), *Caloglossa*, *Catenella* and *Murrayella*. *Murrayella* and *Catenella* are by no means as widely distributed or abundant as the other

genera which almost invariably occur with mangroves and are also commonly associated with saltmarsh vegetation. The red algae associated with mangroves in Australia are listed with their distributions in King and Puttock (1994a). Along with these there is a number of other algae including green algae such as *Rhizoclonium*, *Enteromorpha* and *Percursaria* and phaeophytes' examples of which would be *Dictyotopsis*, *Colpomenia* and *Hydroclathrus* which are often found in mangrove areas and are widely distributed. With the exception of *Dictyotopsis* (Allender 1978) these genera are not restricted to mangrove habitats. Post (1936a) referred to such species as facultative members of the association, and algae which are frequent but not abundant in mangrove algal communities should be considered separately from algae which also grow in adjacent communities on rocky shores or contiguous subtidal seagrass communities and simply continue to grow in the sheltered mangrove after they have been washed in. Examples of such species in eastern Australia include *Sargassum* spp., *Codium* affin. *fragile*, and *Microdictyon umbilicatum* (Velley) Zanardini. In unusual circumstances there may be a local element that is a genuine component of the mangrove algal flora. An example is provided in northern New Guinea where the mangroves, especially *Rhizophora apiculata*, immediately abut the fringing mainland coral reefs and macroalgae normally part of the coral reef community such as *Caulerpa racemosa* (Forrskål) J. Agardh, *Halimeda macroloba* Descaisne and *H. opuntia* (Linnaeus) Lamouroux grow on the aerial roots (King 1990b). A comparable situation occurs at North-West Cape in Western Australia.

Another group of algae associated with mangroves are free-living or unattached forms. These include the free-living *Gracilaria* species which have been described for New Zealand shores by Chapman (1975) and which are certainly more widely spread especially in Australia. In eastern Australia the fucalean *Hormosira banksii* (Turner) Descaisne occurs as a free-living population (King 1981a, b) and similar populations occur in New Zealand. These populations are comparable to the 'ecads' or 'forms' of *Ascophyllum*, *Fucus* and *Pelvetia* found in the salt marshes of the northern hemisphere, in that they exhibit only vegetative reproduction and have a compact densely branched form.

Recent papers from Australia and the region just to the north which either list algae associated with mangroves and their distribution, or from which such information can be derived, are given in Table 1. Further information can be extracted from the taxonomic works discussed below, and some detail is embedded in Post's contributions. Distribution on a local scale, often depicted as zonation on pneumatophores or stilt roots, has been the basis on many descriptive papers in other parts of the world, and an example is provided in the work of Chihara and Tanaka (1988). Various hypotheses involving factors such as salinity, desiccation, and tolerance of sediments in suspension have been put forward to explain the abundance and distribution patterns observed. Beanland and Woelkerling (1983) for example have shown that the degree of shading by the tree canopy could be correlated to changes in frequency distributions of different algae epiphytic on the pneumatophores of *Avicennia marina*, even though species diversity, total cover and biomass do not.

TAXONOMY AND SYSTEMATICS

The taxa most characteristic of mangrove communities in Australia are *Bostrychia*, *Caloglossa*, *Catenella* and *Stictosiphonia*. The global taxonomic treatment of *Bostrychia* (including *Stictosiphonia*) and *Caloglossa* by Post (1936a) has been considerably modified as further collections have become available, new species have been described, and new techniques (culture studies, chemotaxonomy) have been applied, but a classical morphological and anatomical treatment still forms the basis against which the newer data are tested (King and Puttock 1989, 1994b). The genus *Catenella* is in need of further study (Min-Thein and Womersley 1976). Taylor-Wood (1990) and Mostaert (1994) have under-

taken detailed ultrastructural studies of *Bostrychia* and *Caloglossa* respectively using freeze substitution techniques but the data so far are not useful in resolving taxonomic problems.

TABLE 1
Papers on mangrove macroalgal floristics or from which distributional data can be derived, for Australia and coasts to the immediate north (Published since the review of Saenger et al. 1977).

Region and scope of work	References
AUSTRALIA	
general reviews	Saenger <i>et al.</i> (1977), King (1981b), Hutchings and Saenger (1987)
Rhodophyta	King and Puttock (1994)
species list and ecological accounts	
Queensland	Cribb (1979),
New South Wales	King (1981b), King and Wheeler (1985)
Victoria	Davey and Woelkerling (1980, 1985)
South Australia	Beanland and Woelkerling (1982, 1983)
BRUNEI	
species list	King, Puttock and Booth (1992)
INDONESIA	
species list	Tanaka and Chihara (1988a, b)
ecology of macroalgae	Chihara and Tanaka (1988)
PAPUA NEW GUINEA	
species list and ecological notes	King (1990b)

Bostrychia and *Stictosiphonia*

The only broad treatment of the taxonomy of the genus *Bostrychia* since Post (1936a) is that of King and Puttock (1989) who reassessed the genus recognising *Bostrychia* Montagne and the resurrected and emended genus *Stictosiphonia* J.D. Hooker et Harvey. Eleven species of *Bostrychia* and six species of *Stictosiphonia* were recognised and *Bostrychia pinnata* J. Tanaka and Chihara was shown to be a species widely distributed in tropical Australia (King and Puttock 1986). Subsequent publications include a comparative study of the spermatangia in *Bostrychia* (King and Puttock 1991) and further details of the species *B. pilulifera* Montagne which was formerly inadequately known (King *et al.* 1991). Although the major study was based essentially only on morphological and anatomical observations it did include full descriptions of all life-history stages available. In addition multivariate analysis was used to investigate the polymorphic species *B. tenella* (Lamouroux) J. Agardh which is now regarded as including two subspecies *B. tenella* ssp. *tenella* and *B. tenella* ssp. *flagellifera* (Post) R.J. King et Puttock (King *et al.* 1988).

Since the publication of King and Puttock (1989), West *et al.* (1992a) have described a new species, *Bostrychia bispora*, from Darwin, Australia, based on features of reproduction and development in culture. Maggs (1988) has discussed the validity of recognising life-history variants of this nature as separate species. *Bostrychia bispora* is closely related to *B. moritziana* (Sonder ex Kuetzing) J. Agardh but is recognised by asexual reproduction by bisporangia and no sexual reproduction, and its susceptibility to infection by the parasitic red alga *Dawsoniocolax bostrychiae* (Joly and Yamaguishi-Tomita) Joly and Yamaguishi-Tomita. These characteristics cannot be determined on herbarium material so that many sterile collections attributed to *B. moritziana* may be properly this species (King and Puttock 1994a). West *et al.* (1992b) have questioned the separation of *B. moritziana* with monosiphonous lateral branches from *B. radicans* (Montagne) Montagne with only polysiphonous branches (see King and Puttock 1989). They consider that these species cannot be separated reliably in the field: in culture their morphology can be changed from one form to another, and both are susceptible to infection by *Dawsoniocolax bostrychi-*

ae whereas other ecorticate species of *Bostrychia* are not. Molecular systematic approaches may be useful in resolving these and related issues of systematics and biogeography.

The genus *Stictosiphonia* is separated from *Bostrychia* on the basis of the number of tiers of pericentral cells per axial cell, and the pattern of development of subsequent cortication. This separation is partially supported by the distribution of the polyols D-sorbitol and D-dulcitol. These two isomeric hexitols are generally considered to be characteristic of the subfamily *Bostrychioideae* which is comprised of *Bostrychia* and *Stictosiphonia* (Kremer 1976). Investigations by Karsten and Kirst (1989a, b), indicated that this might not be always the case. A subsequent re-evaluation of the polyols showed that in the three species of *Stictosiphonia* examined only D-sorbitol was present, whereas species of *Bostrychia* almost all contained both D-sorbitol and D-dulcitol (Karsten *et al.* 1990). Since that time there have been published a number of exceptions to this simple story, including reports of some populations of *B. radicans* from the east coast of the USA lacking D-dulcitol, and *S. tangetensis* from South Africa containing both D-sorbitol and D-dulcitol (Karsten *et al.* 1992b, 1993, 1994b; West *et al.* 1992b).

Caloglossa

Until the publication of King and Puttock (1994b) there was no overview of the genus *Caloglossa* since the taxonomic synthesis of Post (1936a) and the subsequent examination of the morphology and ecology of the genus (Post 1943). Post (1936A) recognised six species, and although she did not provide detailed descriptions of the taxa considerable information can be extracted from her key. In addition to the six species she also recognised a number of varieties and forms. Subsequently three new taxa were described (*C. lepriurii* var. *angusta* Jao, *C. saigonensis* Tanaka and Pham Hoang Ho and *C. ogasawaraensis* var. *latifolia* Kumano), but none of these has been widely adopted. The first two would be accommodated within *C. lepriurii* (Montagne) J. Agardh as used by Post (1936a), and the last in *C. beccarii* (Zanardini) De Toni. King and Puttock (1994b) have provided a monographic treatment of the genus in which eight species are recognised. In this the prostrate species formerly placed in *C. adnata* (Zanardini) De Toni is recognised as two species, *C. adhaerens* R.J. King and Puttock and *C. bengalensis* (G. Martens) R.J. King and Puttock. No detailed analysis of the range of variation of the widespread and morphoplastic species *C. lepriurii* (Montagne) J. Agardh was undertaken in the study but four subspecies were recognised. The type of detailed study of this complex required, including crossing experiments using Australian material, is being undertaken by Mitsunobu Kamiya with Professor Y. Hara at Tsukuba University in Japan. West *et al.* (1994) have recently recognised a new apomeiotic species, *Caloglossa apomeiotica* West and Zuccarello, closely related to *C. lepriurii* from North America.

ECOPHYSIOLOGICAL STUDIES

The algae of the *Bostrychia* – *Caloglossa* – Association present ideal subjects for the investigation of tolerance to salinity change and desiccation. They grow in environments where there are strong physical gradients related to tide at specific localities, and most of the species also occur over a wide range of salinity along estuaries. For similar reasons ecophysiological research has often been undertaken on saltmarsh and mangrove phanerogams (Adam 1990). Published Australian studies have been concerned largely with the genus *Caloglossa*. Mosisch (1993) studied the effects of salinity on the distribution of *C. lepriurii*, demonstrating its euryhalinity and the presence of distinct salinity ecotypes. In a broader study of six *Caloglossa* species, Karsten and West (1993) investigated the growth pattern and photosynthesis-irradiance curves in relation to salinity and light, and demonstrated an adaptation to shaded habitats for all species.

Members of the genus *Bostrychia* have been much studied in relation to their

capacity to osmoregulate, and special attention has been given to the role of compatible solutes, organic osmolytes such as polyols, amino acids and quaternary ammonium compounds. Compatible solutes balance the high ionic concentration in the vacuole and thus prevent the cytoplasmic enzymes being exposed to high ionic concentrations which would be damaging. In a study of *Bostrychia scorpioides* Karsten and Kirst (1989a) showed that along with concentrations of Na^+ , K^+ and Cl^- , D-sorbitol and D-dulcitol increased with increasing salinity. Although the polyols acted as compatible solutes turgor regulation was not complete. Karsten and Kirst (1989a) suggested that they could be a prerequisite to long term survival in desiccating environments. Desiccation tolerance is a feature of *Bostrychia* species (Post 1963c). In a subsequent study Karsten and Kirst (1989b) reported on the role of inorganic ions and D-sorbitol in the maintenance of the internal osmotic potential of cells of *B. radicans*. The role of both D-sorbitol and D-dulcitol in *Bostrychia* and *Stictosiphonia* have been more widely investigated since (Karsten *et al.* 1990, 1992b, 1993, 1994b; West *et al.* 1992b).

An extensive study of compatible solutes in the genus *Caloglossa* has established that mannitol is a major low molecular weight carbohydrate in that genus (Karsten *et al.* 1992a). The data were obtained with both ^{13}C NMR and HPLC techniques. The result was surprising since mannitol has been regarded as typical of brown algae (Reed *et al.* 1985, Wright *et al.* 1987) and some prasinophytes and haptophytes (Dickson and Kirst 1987) and had not been demonstrated convincingly in any red alga. The variation in mannitol content of field collections of *Caloglossa* in the Sydney (Australia) region support the interpretation that it serves as a compatible solute (Karsten *et al.* 1992a), and in culture the intracellular mannitol concentration in six species of *Caloglossa* has been shown to be directly proportional to the external salinity (Karsten and West 1993). There is some evidence that genetic differences as well as environmental conditions play a role in the accumulation of mannitol.

Further studies (Karsten *et al.* 1994a) on *Caloglossa leprieurii* from different localities using ^{13}C -NMR and ^1H -NMR reaffirm the role of mannitol. The compound 4-hydroxyproline betaine was reported for the first time in *Caloglossa* but was present in only low concentrations in marine specimens and absent from freshwater plants. Digeneaside, the main photosynthetic and reserve product of the Ceramiales (Kirst 1980), was also reported, but the concentration of this and 4-hydroxyproline betaine was not regulated by changes in salinity and they are thought to be unlikely to have a major role in osmoregulation.

An osmotic role for the heteroside floridoside has recently been established in *Catenella nipae* Zanardini from eastern Australia (Karsten *et al.* 1995).

While quantitative changes in organic osmolytes may be sufficient to account for osmotic adjustment in the long term, in macroalgae they are too slow to be of significance in environments with rapid changes in salinity. Water movement into or out of cells resulting in swelling or shrinkage of cells is characteristic of immediate response of algae to osmotic shock. It is the separation of the plasmalemma from the cell wall with plasmolysis which causes damage. The concomitant swelling of the cell wall can prevent this separation as Fischer (1984) suggested for *Caloglossa leprieurii*. Mostaert and King (1993) have shown that in hypersaline conditions up to 5 times seawater concentration the cell wall cross-sectional area of *Caloglossa* from a marine habitat increased from 5.7% to 38.2% of the area occupied by cell contents and cell wall within one hour and in plants from a freshwater habitat from 14.2% to 47.9%. The magnitude and pattern of change in cell wall thickness was consistent with these changes in cell wall having a critical role in osmotic acclimation.

PRODUCTIVITY AND BIOMASS

An important role in community productivity for mangrove macroalgae has been

assumed rather than demonstrated. Biomass is generally low and measured photosynthesis rates of *Bostrychia*, *Caloglossa* and *Catenella* (Karsten and West 1993; Mosisch 1993) are consistent with a range of benthic rhodophytes (King and Schramm 1976). Studies on the free-living *Hormosira* in Botany Bay indicate a conservative production rate of $440\text{g m}^{-2}\text{ y}^{-1}$ though this figure based on seasonal change in biomass fails to take into account loss of fixed carbon by exudation, tissue decay or grazing (King 1981a). A reassessment at the same site in spring 1992, 17 years after the initial observations, indicates that biomass values were virtually unchanged.

Larkum (1981) made a first attempt to quantify production for the entire Botany Bay ecosystem (Sydney, New South Wales) including mangroves but provided no specific estimate of the primary production of mangrove epiphytic algae. It appears that the macroalgae make their major trophic contribution to mangrove ecosystems through detrital food chains, since herbivores are not conspicuous whereas detritivores are often abundant. Whether this is due to the physical environment or whether the particular algae have chemical defence mechanisms against herbivores has not been investigated. Even in ecosystems where grazing molluscs are abundant as in parts of eastern Australia where large numbers of gastropods are present there are no obvious grazing effects (King 1981a).

This brief overview of mangrove macroalgal studies, emphasising recent studies in Australia, highlights a number of shortfalls in our present knowledge. Taxonomic studies have now advanced to the stage where further progress requires the application of newer techniques including culture studies, crossing experiments and the techniques of molecular genetics, in order to resolve relationships between taxa, and to be able to delimit taxa in such morphoplastic species. In the ecological area the factors controlling abundance and distribution are not well understood, though significant progress has been made in understanding response to salinity change. There is also a need for studies on the contribution of the algae to productivity of estuarine and mangrove areas, and an assessment of the way in which this productivity enters the food web.

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